STRUCTURAL DAMAGE AND GALL INDUCTION BY *PEGOMYA CURTICORNIS* AND *PEGOMYA EUPHORBIAE* (DIPTERA: ANTHOMYIIDAE) WITHIN THE STEMS OF LEAFY SPURGE (*EUPHORBIA* × *PSEUDOVIRGATA*) (EUPHORBIACEAE)

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Abstract

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Leafy spurge (*Euphorbia* × *pseudovirgata* [Schur]) is an herbaceous perennial and serious weed of European origin that has been accidently introduced into North America. The European anthomyiid flies *Pegomya curticornis* (Stein) and *Pegomya euphorbiae* (Kieffer) are found on several spurge species in Europe and also attack leafy spurge. The two flies induce identical galls on the subterranean stems of their host plants, and the shoots wilt and die. Eggs are laid on the shoot tip, and the larvae bore into the stem by eating pith which is later replaced by callus. This is a rare example of an insect with both boring and gall-inducing feeding strategies. Galls are induced when larvae feed on the ring of vascular tissue. There is no proliferation of nutritive cells but instead thick layers of gall parenchyma are produced. The vascular connections are broken at the gall level and concentric vascular bundles appear in the cortical and gall parenchyma. After pupation an inner periderm differentiates around the chamber surface.

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Résumé

Accidentellement introduite d'Europe, l'euphorbe feuillue (*Euphorbia* × *pseudovirgata* [Schur]), est en Amérique du Nord, une importante mauvaise herbe vivace. En Europe, plusieurs espèces d'euphorbes, en l'occurrence l'euphorbe feuillue, sont attaquées par les mouches anthomyiides indigènes, *Pegomya curticornis* (Stein) et *Pegomya euphorbiae* (Kieffer). Ces deux espèces entraînent la formation de galles identiques sur les tiges souterraines de leur plantes hôtes, causant ainsi la flétrissure et la mort des pousses. Les oeufs sont placés à l'extrémité de la pousse et la larve creuse dans la tige dévorant la moelle qui sera remplacée par une callosité. Ceci constitue un rare cas de comportement alimentaire où un insecte creuse une tige et entraine la formation d'une callosité. Les galles se forment lorsque les larves se nourrissent dans la zone de tissus vasculaires. Dans la galle, il n'y a pas de prolifération de cellules nutritives mais plutôt production de couches épaisses de parenchyme. Des liens vasculaires sont brisés au niveau de la galle et des bourlets vasculaires concentriques apparaîssent dans le parenchyme cortical et celui de la galle. Après la nymphose, un périderme interne se différencie autour de la surface de la chambre.

Introduction

Flies of the Family Anthomyiidae occur worldwide in distribution, with nearly 565 species known from the Palaearctic region (Hennig 1973) and 600 species known from the Nearctic region (Huckett 1987). Many are phytophagous in the larval stage and bore or mine in the stems, roots, flowerheads, or foliage of their hosts. Some anthomyiids, commonly called root maggots, are serious pests as they feed on the roots of food crops and ornamentals. Other species are saprophagous or scavengers and a few species are known to induce galls. Little is known about the habits of anthomyiids that feed within plant tissues and even less is known of the gall inducers.

Leafy spurge (*Euphorbia* × *pseudovirgata* [Schur]) and cypress spurge (*E. cyparissias* L.) are noxious weeds that have been accidently introduced into Canada and the

northern United States (Watson 1985). As part of a programme to evaluate various insects as potential agents for the biological control of these weeds, two species of gall-inducing anthomyiids were found by the first author on the subterranean shoots of European spurges. One species, *Pegomya euphorbiae* (Kieffer), was found on *E. cyparissias* L., *E. waldsteinii* (Sojak) (*E. virgata* Waldst. and Kit), *E. lucida* Waldst. and Kit., and also on *E. seguieriana* Necker. The other species, *P. curticornis* (Stein), was found exclusively on *E. waldsteinii*.

The Italian anatomist Malpighius first described and illustrated galls of *Pegomya* in 1679; the illustrations were reproduced in Michelsen (1988). This old biological observation remained unconfirmed until the inducer was identified as an anthomyiid by Hering (1968). Hennig (1973) used the name *P. argyrocephala* (Meigen) in his monograph of the genus. Recent studies by the first author on the biology of *P. curticornis* and *P. euphorbiae* resulted in a large collection of galls at various stages of development.

When the first author collected and reared shoot-boring and gall-inducing anthomyiids on European spurges, it was assumed that a single species, *P. argyrocephala*, was present. However, because Hennig (1973) had suggested that *P. argyrocephala* was variable and that it likely was an aggregate of sibling species, only flies reared from the closely related European *E. waldsteinii* were cultured in 1985 and 1986 on the North American weed *E.* × *pseudovirgata*. In 1987, with the acquisition of additional specimens from other European spurges, Michelsen (1988) determined that there are five species of spurge-boring *Pegomya*, all of which are distinguished by the terminalia. Two of the species were new and the other three, including *P. euphorbiae* and *P. curticornis*, were redescribed. All the flies reared from *E. cyparissias* were *P. euphorbiae* but *P. curticornis* and *P. euphorbiae* were both reared in variable proportions from the *E. waldsteinii* populations in Hungary. This meant that the plants of leafy spurge previously cultured for study of gall development had been infested indistinctly by two species, *P. curticornis* and *P. euphorbiae*. However, the galls of these closely related species could not be distinguished and we decided to present our results as if the galls were induced by a single species. The purpose of this paper is to describe the structural damage caused by the larvae of *P. curticornis* and *P. euphorbiae* as they bore and gall the shoots of North American leafy spurge.

Pegomya curticornis and *P. euphorbiae* are univoltine and have been found on *E. waldsteinii* only in Hungary and eastern Austria. Techniques for rearing these two species are given in Gassmann (1987). The adults emerge in March–April from puparia that overwinter within galled shoots. Oviposition takes place 3–4 days after emergence. Eggs are laid singly or in small groups between the immature leaves and floral parts at the tip of developing shoots. Upon eclosion, the larva bores down the centre of the shoot reaching the base in about 4 weeks where its feeding activity induces gall formation. The first sign of gall development was observed 30–40 days after oviposition. Under field conditions, the third and final larval instar is reached within 3 weeks and development is completed within 60–80 days. A puparium is formed inside the gall in June. Galled shoots wilt and eventually die, thus establishing the potential of *P. curticornis* and *P. euphorbiae* as biocontrol agents of leafy spurge and cypress spurge in North America.

Leafy and cypress spurge are herbaceous perennials of European origin that have been accidently introduced into North America. There are about 80 perennial species in Europe (Smith and Tutin 1968). Those of the *E. esula* L. group, most of which are native to central and southeastern Europe, include several adventive species and hybrids in North America. Two of these, the hybrid leafy spurge (*E.* × *pseudovirgata* [Schur] Soo) and cypress spurge (*E. cyparissias* L.), are aggressive weeds rapidly spreading in Canada and the American midwest (Watson 1985). They preferably invade unmanaged areas and pastures where they replace the native flora (Watson 1985). These spurges also contain a latex that is toxic to many grazing animals (Watson 1985).

Materials and Methods

Tissues from approximately 50 *Euphorbia* × *pseudovirgata* plants with eggs, larvae, and pupae of *P. curticornis* or *P. euphorbiae*, along with pieces of unattacked stems and roots from about 15 plants, were obtained at the CABI Institute of Biological Control (CIBC) in Delemont, Switzerland. About 15 mature galled shoots of *E. waldsteinii* also were collected from the field for comparison with galled shoots of *E.* × *pseudovirgata*. All tissues were fixed and stored in Formalin – acetic acid – alcohol (FAA). Subsequently they were dehydrated in a tertiary-butyl alcohol series and embedded in paraffin (Jensen 1962) at Laurentian University in Sudbury, Ont. All tissues were sectioned at 8 μm with a rotary microtome and stained with safranin-fast green. Starch was localized with IKI (Jensen 1962).

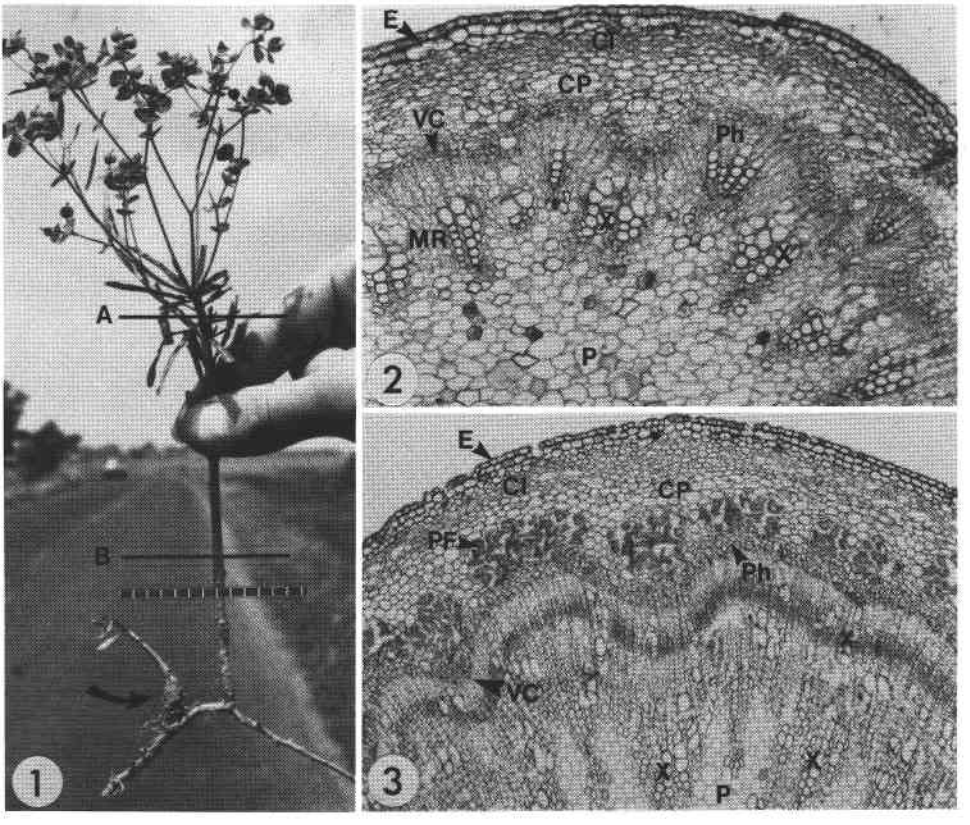
Results

Gall Description. Mature galls of *Pegomya curticornis* and *P. euphorbiae* are slight swellings of the shoots (Fig. 1), about 10–15 mm long and 4–7 mm wide. The surface is always smooth. Immature galls are light green or white and mature galls are brown. Mature galls with pupae have a horizontal slit used by the adult as an escape route. Galls are always found on the subterranean part of the stem. In most cases they are formed at the base of shoots at the point of attachment to the rhizomes (see Malphigius' illustrations in Michelsen 1988). The fact that most galled shoots wilt and break off at ground level makes locating mature galls in the field difficult.

Anatomy of Stems. Stems of leafy spurge frequently extend from 2 to 20 cm below the soil surface before the stem-to-root transition is reached. The upper parts of the stems of leafy spurge (Fig. 2) are anatomically different from mature stems either at or below the ground surface (Fig. 3). Stems in the upper part of the plant exhibit limited secondary growth (Fig. 2), whereas stems in the lower part of the plant exhibit more extensive secondary vascular tissue (Fig. 3) and as a result are somewhat woody.

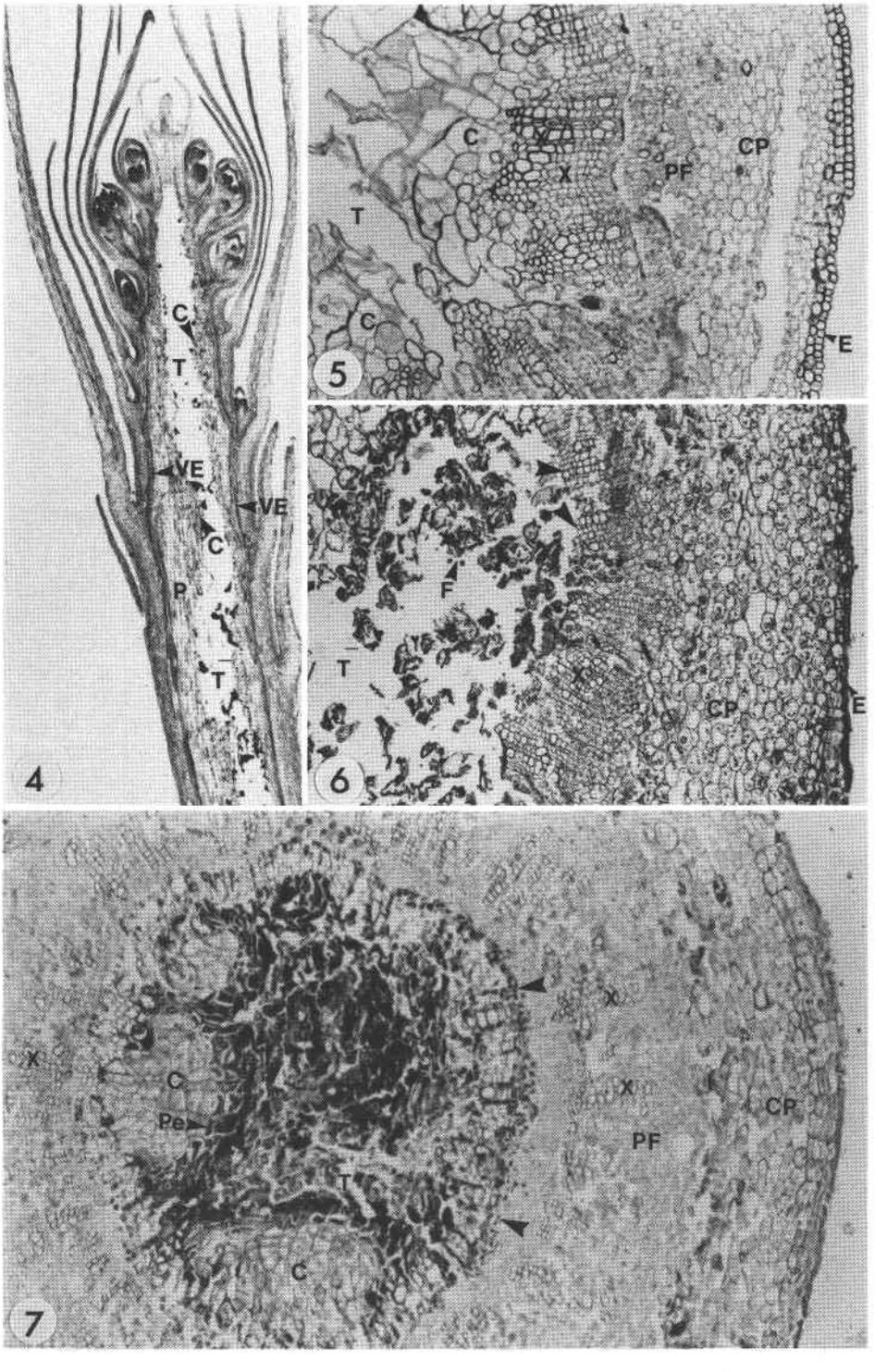
Stems about 10 cm below the shoot tip consist of an epidermis, cortex, vascular bundles, a cambial zone, and an inner region of pith (Fig. 2). The pith consists of thin-walled parenchyma cells of varying size, with intercellular spaces. Vascular tissue is arranged in an irregular sinuous ring of large and small wedge-shaped vascular bundles (Fig. 2). The parenchyma forms broad primary medullary rays between the vascular bundles. The cortex is a broad layer of small, circular, thin-walled, chlorophyll-bearing parenchyma cells with intercellular spaces, along with laticifers, which are branched cells containing milky latex. The outer cortex consists of a collenchymatous sheath. The single epidermal layer has thickened walls and a thick cuticle.

The lower part of the stem (Fig. 3), at or beneath the ground surface, differs from the stem above because of secondary growth. The cambium, which starts its activity when the plants are about 20 cm tall, forms radial files of secondary xylem elements that increase in number outward so that the breadth of the medullary rays diminishes correspondingly. The cambium inward mostly forms sclerenchymatous cells, which are rather small, mostly quadrangular or rectangular in cross section. Here the wood has the form of a strong cylinder of mechanical tissue, with vessels and some parenchyma (Fig. 3). There is less pith than above (Fig. 2). Outside the cambium and secondary phloem, there are small to large groups of very thick-walled sclerenchyma cells and phloem fibres. The cortex consists of small, round, thin-walled, chlorophyll-bearing (above the ground surface only) parenchymatous cells, with intercellular spaces of various sizes. Laticifers are present in the cortical parenchyma, mostly in the inner side. The laticifers run the length of stems. The starch content of the cortical and pith parenchyma is variable. Starch increases with stem age and is more conspicuous in the lower region. The epidermis is not present in underground regions of the stem because it is replaced by a few layers of cork cells.



FIGS. 1–3. Habit and anatomy of *Euphorbia* × *pseudovirgata*. 1. Habit of normal (right) and galled (arrow) *Euphorbia* × *pseudovirgata* shoots. Lines (A and B) indicate the approximate areas from which sections shown in Figs. 2 and 3 were taken. Broken line indicates ground level. 2. Cross section of stem from upper part of plant (line A in Fig. 1) after a short period of secondary growth. Note the thin-walled parenchymatous pith cells and the smaller cortical parenchymatous cells. Note also the single irregular sinuous ring of small and large wedge-shaped vascular bundles. ×35. 3. Cross section of stem from near ground level (line B in Fig. 1) with radial rows of secondary xylem elements. Note also the thick-walled sclerenchymatous cells of the phloem fibres and that the pith cells are smaller than those above. ×25. *Cl*, collenchyma; *CP*, cortical parenchyma; *E*, epidermis; *MR*, primary medullary rays; *P*, pith; *Ph*, phloem; *PF*, phloem fibres; *VC*, vascular cambium; *X*, xylem.

FIGS. 4–7. Sections of shoots of *Euphorbia* × *pseudovirgata* inhabited by boring larvae of *Pegomya curticornis* or *P. euphorbiae*. 4. Longitudinal section of shoot tip showing the path of a freshly hatched larva. Note that the larva has restricted its feeding to the central pith. ×6.7. 5. Cross section of stem near the ground surface occupied by larva about 30 days after oviposition. Shoot fixed at day 38. A third-instar larva was found 7 cm below the section. Note the callus forming around the feeding channel. ×57. 6. Cross section of stem near the shoot base 37 days after oviposition. A third-instar larva was found about 1 cm above this section. Note frass in the tunnel and absence of callus around the feeding channel. Note also that some feeding occurs on the xylem vessels (arrows). ×41. 7. Cross section of stem above a mature gall. Note the clusters of callus cells protruding into former larval tunnel along with frass. Also note the new cambium (arrows). ×50. *C*, callus; *CP*, cortical parenchyma; *E*, epidermis; *F*, frass; *P*, pith; *Pe*, periderm; *PF*, phloem fibres; *T*, tunnel; *VE*, vascular elements; *X*, xylem.



Boring Stage. Oviposition occurs in early April when the plants are about 20 cm high. Eggs are laid between the developing leaves or floral bracts of the shoot tip. Upon hatching the larvae bore into the developing stem by tunnelling directly into and through young leaves or bracts of the shoot tip. The first indication of morphological change to the host plant is an atypical shape of the shoot tip and the cessation of shoot growth. Immature leaves at the tip are often distorted.

The larvae bore internally down into the shoot (Fig. 4) by eating and chewing the parenchyma cells of the pith. Vascular tissues are rarely eaten at this stage. Pith cells adjacent to the tunnel divide and differentiate into callus a few days after the larva has passed (Fig. 5). The third-instar larvae reach the shoot base in about 3–4 weeks. They often penetrate 1–2 cm below the ground surface but turn back up the tunnel, consuming remaining pith and freshly proliferated callus. Regions of the stem that are repeatedly visited by the larva become cluttered with frass (Fig. 6). This movement back and forth within the stem near the ground surface continues for 1–2 weeks until all pith and callus are consumed, exposing xylem vessels.

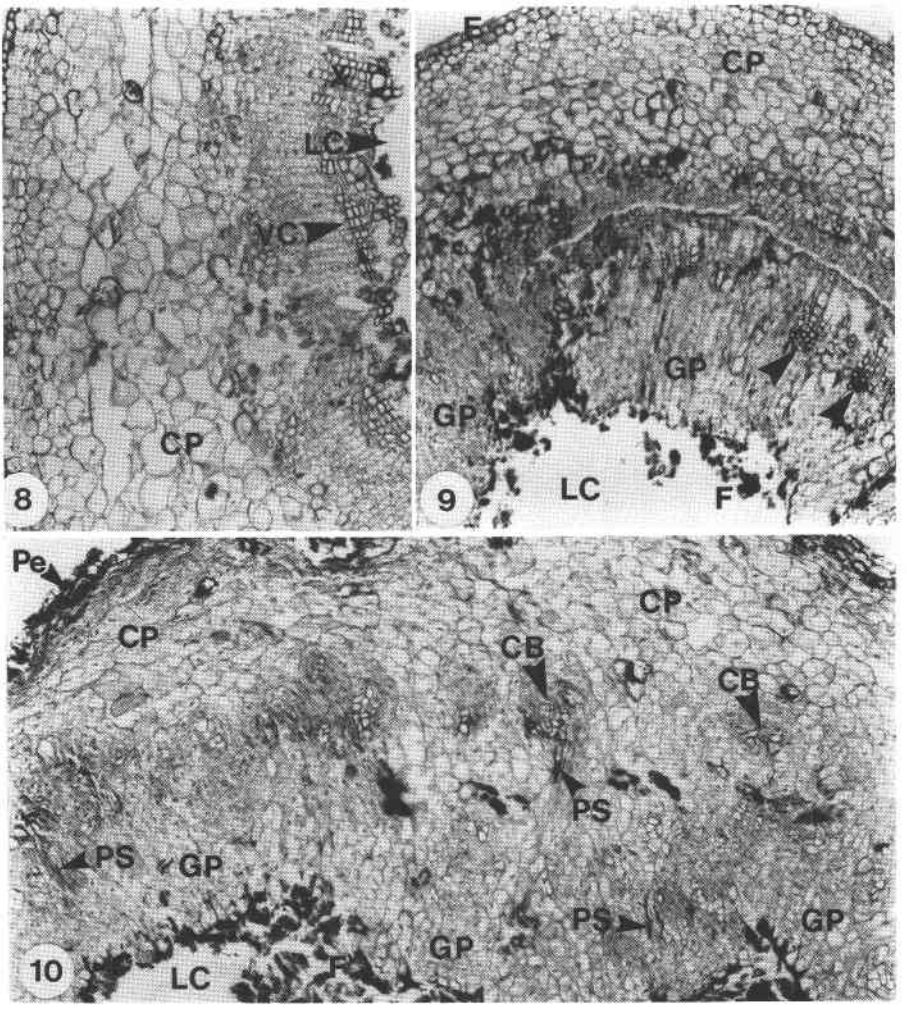
The callus in sections of the tunnel not revisited by the larva continues to proliferate long after the larva has passed. In some areas the callus proliferates in a series of protrusions composed of numerous layers of cells (Fig. 7). In such regions the callus cells adjoining the tunnel become taniferous-like cork cells and a second cambium may appear from which vascular tissue is produced (Fig. 7).

Gall Development. After 4–5 weeks, the larvae stop moving up and down the stem and become sedentary in a region 1–5 cm below the soil surface. Any callus that had formed in this region as a result of previous boring is consumed and the larvae begin feeding on the ring of vascular elements (Fig. 8). In areas where the vascular tissues are almost completely consumed, the remaining vascular cambium and cortical cells proliferate to form thick layers of parenchyma cells referred to here as gall parenchyma (Fig. 9). In some cases, proliferating gall parenchyma forms between the remaining cells of the vascular ring and the larval chamber (Fig. 9). The larvae feed exclusively on the gall parenchyma, except when they chew through to the cortex or they encounter secondary vessels. Cells of the gall parenchyma apparently divide and enlarge in a uniform manner and as a result, the zone appears as a mass of tightly packed cells, all of which are smaller than cells of the cortex (Fig. 9). Cells throughout the gall parenchyma, including those lining the larval chamber, are similar; however, some have an enlarged nucleus and nucleolus and many have dense cytoplasm.

As the gall parenchyma matures and enlarges, procambial strands differentiate within the zone (Fig. 10). Some procambial strands extend almost to the edge of the larval chamber (Fig. 10). At the same time, by 60 days after oviposition, concentric vascular bundles begin to differentiate within the proliferating gall parenchyma and cortical parenchyma. No laticifer cells were found in the gall parenchyma. Expansion of the gall parenchyma and cortical parenchyma is responsible for the increased diameter of galled stems compared with corresponding areas of unattacked stems. The epidermal cells of galled shoots elongate tangentially and often are irregular in size and shape. As the gall matures, the epidermis of the subterranean tissues is replaced by a few layers of cork cells (Fig. 10).

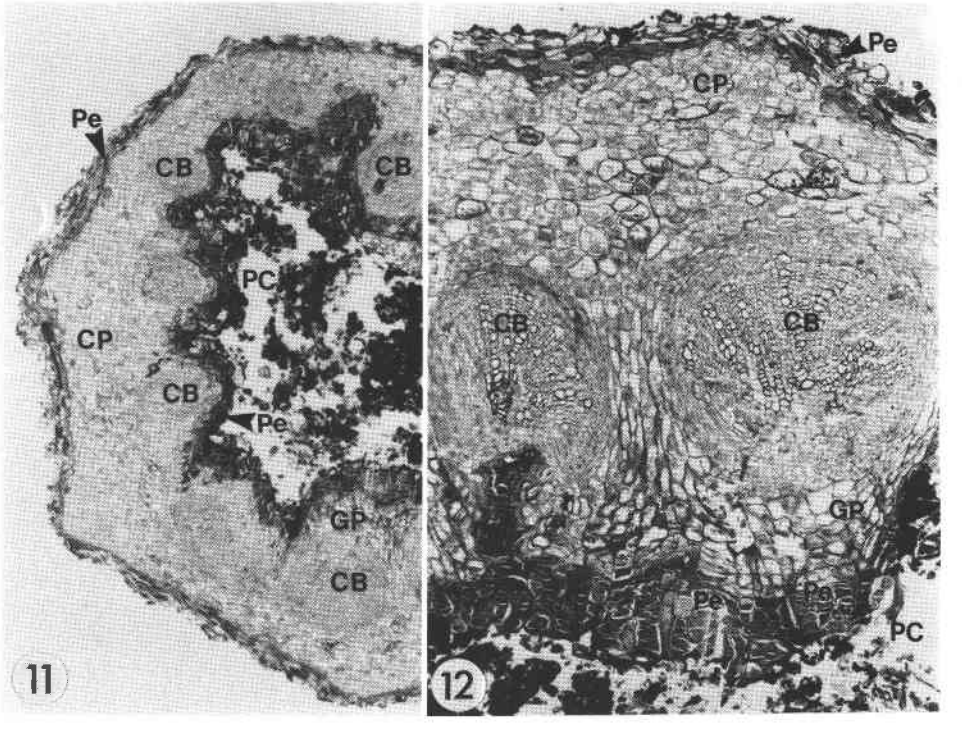
Gall parenchyma continues to proliferate as the larva feeds and as the gall reaches its final size, the interior surface of the larval chamber becomes convoluted (Fig. 11) and lined with damaged cells and frass. By 80 days after oviposition the concentric vascular bundles are well differentiated (Figs. 11 and 12). These new bundles have a central xylem and an external phloem.

Most galls with larvae ready to pupate have some gall parenchyma, although all the gall parenchyma is sometimes consumed. Prior to pupation, the larva chews an escape



FIGS. 8–10. Sections of immature galls. 8. Section of subterranean stem inhabited by third-instar larva at day 38, at the beginning of gall initiation. Note that all pith and most vascular tissue has been consumed. Also note that the cortical parenchyma consists of irregular cells. ×75. 9. Section of gall inhabited by third-instar larva at day 41. Note that nearly all vascular tissue has been consumed and the larval chamber is lined with proliferating gall parenchyma. Some vascular tissue is present in the central part of the section (arrows), but it also is isolated from the larval chamber by gall parenchyma. ×45. 10. Section of gall inhabited by third-instar larva at day 56. Note the procambial strands in the gall parenchyma. Also note that concentric vascular bundles are forming within the zone of gall parenchyma. ×36. *CP*, cortical parenchyma; *CB*, concentric vascular bundles; *E*, epidermis; *F*, frass; *GP*, gall parenchyma; *LC*, larval chamber; *PS*, procambial strands; *Pe*, periderm; *VC*, vascular cambium; *X*, xylem.

route through the gall parenchyma and cortex leaving only a thin layer of cork cells for the adult to push through the following spring. The larva pupates in the chamber. Once the larvae cease to feed, an inner periderm differentiates over the surface of the larval chamber (Fig. 12), similar to that on the outside surface. A cork cambium differentiates near the inner chamber surface and several layers of tannin-filled cells are centripetally produced (Fig. 12). Pupation occurs in the second half of June, but the gall tissues stay alive until the following spring.



FIGS. 11–12. Sections of mature galls. 11. Cross section from upper part of mature gall with pupa at day 80. Note that all primary and secondary vascular tissues have been consumed and that new concentric vascular bundles have formed within the gall and cortical parenchyma. Note also that a thick layer of periderm has formed around the pupal chamber. ×31.5. 12. Section of cells from the gall in Fig. 11 showing new concentric bundles and periderm lining the pupal chamber. ×52.5. *CP*, cortical parenchyma; *CB*, new concentric vascular bundles; *GP*, gall parenchyma; *PC*, pupal chamber; *Pe*, periderm.

Discussion

Pegomya curticornis and *P. euphorbiae* are unusual as they belong to two feeding guilds. For the first 4–5 weeks of their larval development, they feed as borers; when they feed within the lower part of the subterranean stem for 6–8 weeks, they are gall inducers. It is appropriate to refer to the tunnelling larvae as borers and not miners. According to Hering (1951), miners are insects that feed in leaves just below the surface, whereas borers are insects that feed deep within plant organs such as stems and roots (Rathcke 1976). When larvae of *P. curticornis* and *P. euphorbiae* cause the swelling of stems and feed on proliferating cells that they have induced, they are clearly gall inducers.

Most gall insects do not bore but induce the proliferation of cells at the oviposition site (Meyer and Maresquelle 1983). However, gall-inducing tephritids often tunnel a short distance from shoot tips to gall induction sites (Lalonde and Shorthouse 1984).

The two feeding strategies developed by larvae of *P. curticornis* and *P. euphorbiae* result in the consumption of at least four types of plant cells. The first-, second-, and young third-instar larvae consume only pith cells as they form the initial tunnel; however, when they return to older parts of the tunnel third-instar larvae are able to feed on proliferating callus. After 4–5 weeks, older third-instar larvae become sedentary in the lower part of the subterranean stem and consume secondary vessels and then the proliferating gall parenchyma mass. The larvae move up and down the lower part of the stem for a

short time, presumably waiting for the appearance of gall parenchyma. Callus is formed in the lower stem soon after the larvae have consumed all the pith, but it too is soon consumed. We assume that the larvae would starve if they were unable to induce the production of gall parenchyma.

The proliferation of callus from pith and interfascicular parenchyma is apparently a plant reaction to insect feeding. Callus is commonly associated with regions of plant organs that have been damaged or wounded (Lipetz 1970; Kahl 1985). Although callus formation usually occurs on externally damaged tissues, it does occur near the feeding sites of other endophytophagous insects (Shorthouse and Lalonde 1984). In nearly all cases, callus is a sealing barrier composed of physiologically altered cells that partition the damaged and healthy regions. Layers of callus then differentiate in the area behind the physiologically altered cells and the whole region is then referred to as a wound callus zone (Shorthouse and Lalonde 1984). A striking feature of some mature callus of leafy spurge is its accumulation of densely staining tannin-like substances. The accumulation of tannin-like compounds in regions of plants that have been wounded is well known (Meyer and Maresquelle 1983).

The other apparently wound-related response by tissues of attacked leafy spurge is the appearance of periderm-like layers of cells along the inner surface of the larval chamber. In most herbaceous dicotyledons, periderm is a protective tissue of secondary origin that replaces the epidermis in stems and roots (Esau 1977; Kahl 1982). It most commonly forms externally as a normal part of aging; however, it can form due to mechanical wounding or invasion of parasites (Struckmeyer and Riker 1951). Periderm also is known to form in the xylem of some plants (Moss and Gorham 1953). According to Kahl (1982), the formation of wound periderm is similar to that of callus, but the extension growth is usually restricted to cells beneath the wound surface (phellogen cells). The periderm-like cells in mature galls also contain tannin-like substances which may be an induced resistance against further attack (Swain 1977).

The examination of all sections of galls from leafy spurge, supplemented by studies of the gall of *E. cyparissias* (unpublished data), do not show a difference in the structural damage and gall anatomy invoked by *P. curticornis* and *P. euphorbiae* on North American leafy spurge. This is unusual because even closely related species of gall insects usually induce structurally distinct galls (Shorthouse 1982). Also, the anatomy of galls obtained on leafy spurge in the laboratory is similar to that observed on *E. waldsteinii* collected in the field.

Galls induced by *P. curticornis* and *P. euphorbiae* are simple compared with those of most other insects. Although they are histoid galls (Meyer and Maresquelle 1983), the lack of differentiated layers of cells classifies them as kataplasmic rather than prosoplasmic. These gall insects do not induce the proliferation of highly specialized nutritive cells common in more advanced galls (Rohfritsch and Shorthouse 1982; Shorthouse 1986). The lack of specialized nutritive cells may be compensated for by the nutrients brought directly to the larval chambers by the vascular tissue. According to Rohfritsch and Shorthouse (1982), the vascular tissues of galls show the histochemical characteristics of nutritive tissues. Also, the fly does not induce the formation of new cells in ordered layers characteristic of prosoplamic galls (Rohfritsch and Shorthouse 1982). The gall parenchyma induced by these two *Pegomya* resembles the callus cells induced by *Rhinocyllus conicus* Froelich (Shorthouse and Lalonde 1984). The ability to induce specialized nutritive cells is uncommon among chewing insects. Galls of these *Pegomya* are therefore of the primitive type but the appearance of concentric vascular bundles in the cortical and gall parenchyma indicates a trend toward more complex structures.

Another peculiar feature of host modification by these two *Pegomya* is the induction of cambium within the zone of secondary vessels above and below the site of the gall. Apparently this host reaction also is caused by the larvae feeding on vascular tissue and is an attempt by the plant to renew vascular connections in the damaged area.

The appearance of procambial cells in the gall parenchyma is common to the galls of many insects (Meyer and Maresquelle 1983). According to Bunning (1965) plants form new vascular bundles when new parenchyma is removed from the influence of existing stem vascular bundles. The new conducting tissue is clearly oriented toward the larval chamber in advanced galls (Meyer 1969) suggesting that the insect also influences the production of new vascular tissue. This may be the case at least in the early growth phase of the *Pegomya* galls when the procambial cells are directed toward the feeding sites. In kataplasmic galls, the insect usually induces the disorganization of conducting tissues (Meyer and Maresquelle 1983). The appearance of concentric vascular bundles (Fig. 12), called amphicribral bundles by Esau (1977), in the gall parenchyma apparently is a response to a severed vascular system.

Sectioning host tissues inhabited by *P. curticornis* and *P. euphorbiae* provides the type of information on host damage that Harris (1981) stated is needed to evaluate potential biocontrol agents. Damage by larvae of *Pegomya* is clearly seen in the apical region of the stem as the early larvae bore through the meristem and pith. Boring arrests shoot growth and suppresses seed production (unpublished data). The proliferation of callus within tunnels represents a diversion of host carbohydrates; however, the most severe damage occurs when the third-instar larva consumes secondary vessels in the subterranean part of the stem. In nearly all cases, the attacked plants wilt and all tissues above the gall die. The proliferation of gall parenchyma and the growth of concentric vascular bundles to replace the vascular tissue severed by the larvae represent a redistribution of plant resources away from growth and reproduction. In our opinion the two species of *Pegomya* should be used as agents for the biological control of leafy spurge in North America.

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